

Neotoma fuscipes. By L. N. Carraway and B. J. Verts

Published 6 November 1991 by The American Society of Mammalogists

Neotoma fuscipes Baird, 1858

Dusky-footed Woodrat

Neotoma fuscipes Baird, 1858:495. Type locality "Petaluma, [Sonoma Co.], California."

Neotoma macrotis Thomas, 1893:234. Type locality "San Diego, [San Diego Co.], California."

Neotoma splendens True, 1894:1. Type locality "Nicasio, [Marin Co.], California."

Neotoma monochroua Rhoads, 1894:67. Type locality "Grant's Pass, Josephine Co., Oregon."

CONTEXT AND CONTENT. Order Rodentia, Suborder Myomorpha, Superfamily Muroidea, Family Muridae, Subfamily Sigmodontinae, Genus *Neotoma*, Subgenus *Neotoma* (Burt and Barkalow, 1942; Carleton, 1980; Carleton and Musser, 1984; Hall, 1981). Eleven subspecies are recognized as follows (Hall, 1981; Hooper, 1938):

N. f. annectens Elliot, 1898:201. Type locality "Portola, San Mateo Co., California" (*affinis* Elliot is a synonym).

N. f. bullator Hooper, 1938:225. Type locality "2 miles south of San Miguel, 620 feet altitude, San Luis Obispo County, California."

N. f. fuscipes Baird, 1858, see above (*splendens* True is a synonym).

N. f. luciana Hooper, 1938:229. Type locality "Seaside, Monterey County, California."

N. f. macrotis Thomas, 1893, see above.

N. f. martirensis Orr, 1934:110. Type locality "Valladares, altitude 2700 feet, Sierra San Pedro Mártir, Lower California, Mexico."

N. f. monochroua Rhoads, 1894, see above.

N. f. perplexa Hooper, 1938:224. Type locality "Sweeney's Ranch, 22 miles south of Los Banos, Merced County, California."

N. f. riparia Hooper, 1938:223. Type locality "Kincaid's Ranch, 2 miles northeast of Vernalis, Stanislaus County, California."

N. f. simplex True, 1894:2. Type locality "Fort Tejon, [Kern Co.], California" (*dispar* Merriam, *cnemophila* Elliot, and *mohavensis* Elliot are synonyms).

N. f. streator Merriam, 1894:124. Type locality "Carbondale, Amador Co., California."

DIAGNOSIS. *Neotoma* can be separated from other sympatric or parapatric rodents by occlusal surfaces of the molars being flat and prismatic, with the middle prism of M1 and M2 extending completely across the teeth (Fig. 1), openings of the ears not covered with hair, and rings of scales on tail obscured (Ingles, 1954). *N. fuscipes* (Fig. 2) can be separated from *Neotoma* with which it is sympatric or parapatric by its grayish-brown dorsum, usually pale or white venter, sooty-colored pelage on top of the hind feet, and the faintly bicolored, scanty haired, terete tail covered with short, dark-sooty colored hairs (Howell, 1926; Jameson and Peeters, 1988). *N. lepida* has a ventral pelage composed of hairs gray at the base and white at the tip and a distinctly bicolored tail; *N. cinerea* has a pale gray dorsum and a long bushy tail; *N. albigula* has throat hairs white to the base and a bicolored tail (Jameson and Peeters, 1988).

Neotoma fuscipes has a longer tail, hind foot, and ear than *N. lepida*, and a longer ear than *N. albigula* (Jameson and Peeters, 1988). *N. fuscipes* can be separated from *N. cinerea* by an open sphenopalatine vacuity in adults, lack of a reentrant angle on the anterior face of M1, and lack of a ventral dermal gland (Howell, 1926). The mystacial and superciliary vibrissae tend to be shorter in *N. fuscipes* than in *N. cinerea*. In *N. fuscipes* the mystacial vibrissae are black; however, in *N. cinerea* they have either white tips with black bases or are all white (Howell, 1926). *N. fuscipes* has one 40-mm-long vibrissa between the ear and eye (Howell, 1926).

The lateral diameter of the base of the baculum of *N. fuscipes*

is greater (3.50-3.62 mm) than in *N. albigula* (2.82-3.50 mm), *N. cinerea* (1.1-1.7 mm), and *N. lepida* (1.8-2.2 mm—Burt and Barkalow, 1942). *N. fuscipes* has a straight baculum (Fig. 3), whereas in *N. albigula* the baculum is moderately curved ventrally (Burt and Barkalow, 1942).

GENERAL CHARACTERS. *Neotoma fuscipes* is a medium-sized rat-like form with black protruding eyes, soft and smooth pelage, and a long tail. It has scanty haired pinnae (Fig. 2) with a small tragus and a double antitragus (Howell, 1926). *N. fuscipes* has reddish-orange eye shine (Vestal, 1938). The hind feet are longer than the forefeet, have five toes, and six plantar tubercles; the forefeet have four toes and five plantar tubercles (Vestal, 1938). Tracks consist of impressions of the plantar tubercles and the terminal digital tubercles (Vestal, 1938).

Interspersed among the 15-mm-long hairs on the dorsum and sides are guard hairs ca. 20 mm long. On adult males, hairs at midventer are coarse and ca. 40 mm long (Howell, 1926). The pelage color of subspecies of *N. fuscipes* along the Pacific Coast is darker than that of inland forms (Goldman, 1910).

Ranges of external and skull measurements (in mm) of females and males combined from throughout the range are: total length, 335-468; length of tail vertebrae, 160-227; length of hind foot, 34-47; length of ear, 24-36; basilar length, 38.7-44.7; depth of skull, 14.4-19.1; breadth of rostrum, 6.1-8.3; breadth of bulla, 7.1-9.1; zygomatic breadth, 21.8-28.1; length of nasals, 16.1-21.4; least interorbital breadth, 4.9-6.6; and length of upper molar series, 7.8-10.3 (Bailey, 1936; English, 1923; Gander, 1929; Goldman, 1910; Hooper, 1938; Howell, 1926; Ingles, 1965). The range in body mass of *N. f. streator* (Grinnell and Storer, 1924) was 206-247 g. Other references to body mass of *N. fuscipes* include 200-250 g (Kofoid et al., 1935), 311.8 g (Bailey, 1936), and 186.7 g (Lee, 1963). Mean (\pm SE) body masses of winter and summer samples of *N. fuscipes* in California were significantly different (221.4 ± 19.4 g, $n = 8$; 185.6 ± 10.7 g, $n = 10$, respectively—Stallone, 1979). Brain mass of *N. fuscipes* calculated from volume of the braincase averaged 3.3 g (Mace et al., 1981).

DISTRIBUTION. *Neotoma fuscipes* occurs (Fig. 4) in a narrow band from the Columbia River south through the interior valleys of Oregon, thence along the Pacific Coast and through the interior valleys of California into northern Baja California (Hall, 1981).

FOSSIL RECORD. Remains of *N. fuscipes* have been found at a few late Pleistocene sites in California, including Hawver Cave, Eldorado Co. (Stock, 1918); McKittrick, Kern Co.; Newport Bay Mesa, Orange Co.; and San Pedro, Los Angeles Co. (Kurtén and Anderson, 1980; Miller, 1971). Earliest records are from the Sangamonian (Kurtén and Anderson, 1980).

FORM AND FUNCTION. Densities of limb-bones (\pm SD) for *N. fuscipes* ($n = 6$) were femur, 1.20 ± 0.16 ; tibia and fibula, 1.31 ± 0.20 ; humerus, 1.29 ± 0.14 ($n = 5$); and radius and ulna, 1.40 ± 0.27 (Stein, 1989). Pelvis (>36.0 mm long) of adult females and males may be separated by the formula $Y = 2.5X - 1.79$, where Y = least width of the pubis and X = the ratio of the length from the acetabulum to the most posterior point of the ischium: length from the acetabulum to the most posterior point of the pubis (Dunmire, 1955). Means and ranges for females and males (in parentheses) for Y were: 1.2, 1.0-1.5 (1.6, 1.2-1.8) and for X were: 1.35, 1.21-1.42 (1.24, 1.15-1.36). Pubes were separated at the symphysis in all adult females. There were no discernable differences of the pelvis among *N. f. annectens*, *N. f. monochroua*, or *N. f. streator* (Dunmire, 1955). The dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16 (Hall, 1981).

Males have large and diffuse ampullary glands connected to the distal 5-7 mm of the corresponding vas deferens by numerous

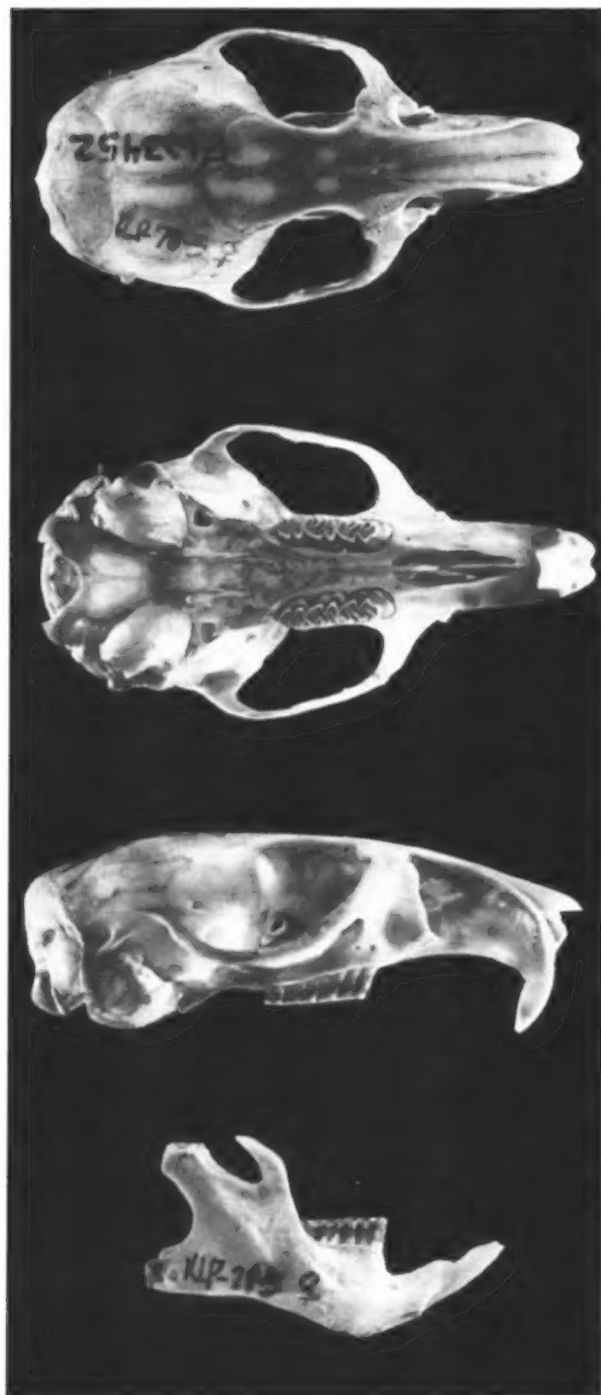


FIG. 1. Dorsal, ventral, and lateral views of the cranium, and lateral view of the mandible of an adult female *Neotoma fuscipes* (OSUFW [Oregon State University Department of Fisheries and Wildlife] 3452) from 1 mi S, 1.5 mi E Hoskins, Benton Co., Oregon. Occipitonasal length of skull is 46.1 mm.

ducts. Two pairs of prostate glands measure 12 by 6 mm. The spread of the heavily branched tubules of the seminal vesicles is 25–30 mm (Arata, 1964). Bulbs of corpus spongiosum and a pair of Cowper's glands are present (Howell, 1926).

The glans penis of *N. fuscipes* is unusual for neotomines because of its flowerlike structure that comprises the terminal half of the distal tract and occupies only a small portion of its prepuce cavity. The glans penis is composed of a squat, lobate body, cylindrical at the base and flared and lobate distally, and a distal tube. It has a pair of ventral lobes, separated by a midventral longitudinal groove and a full-length raphe, and a distally concave dorsolateral pair of lobes that form a basin from which extends the tubular

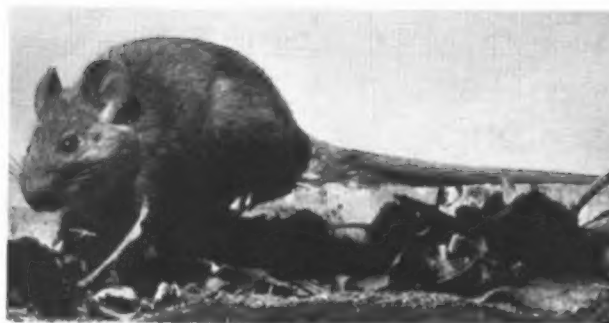


FIG. 2. Photograph of *Neotoma fuscipes monochrourea* (juvenile female, from 1.6 km N, 1.6 km E Adiar Village, T10S, R4W, SE¼ Sec. 20, Benton Co., Oregon).

process (Hooper, 1960). The slightly protractile tubular process is expanded medially. The only armature on the surface of the glans penis is a few small tubercles on the dorsal and lateral surfaces. The contractile tissue in the meatus urinarius gives rigidity to the tip of the distal tube. In the urethra are "a short midventral flap equipped with a pair of minute processes" and a "long attenuate cone of soft tissue that emerges from the middorsal wall of the urethral canal and extends into the distal tube" (Hooper, 1960:9).

The baculum of *Neotoma fuscipes* is short, broad, and symmetrical in outline (Fig. 3). The basal end, as viewed from the proximal aspect, is dumbbell shaped and deeply concave in both dorsal and ventral profiles (Burt and Barkalow, 1942). The baculum of *N. f. annectens* is 5.02–5.50 mm long (Burt and Barkalow, 1942); however, a mean of 2.0 mm for *N. f. luciana* and *N. f. macrotis* has been reported (Hooper, 1960). The lateral and dorsoventral diameters (in mm) are: 3.50–3.62 and 1.80–1.92 at the base and 0.90–0.99 and 0.80–0.89 near midshaft (Burt and Barkalow, 1942). The baculum is situated well within the dorsal section of the glans penis and is immobile (Hooper, 1960).

Spermatozoa are about 125 μ m long, have a sharply curved and pointed head, and a long slender tail (Wood, 1935). The vaginal fluid contains leucocytes and epithelial and cornified cells suspended in thin, pearly mucus (Wood, 1935). There are four inguinal mammae (English, 1923; Wood, 1935); however, one instance of five mammae (two left, three right) was reported (Wood, 1935).

During the breeding season, testosterone concentrations of ≤ 1.75 ng/ml were significantly different from the ≤ 0.75 ng/ml during the nonbreeding season (Caldwell et al., 1984). For castrated males these values (0.21 ± 0.07 ng/ml, 0.24 ± 0.05 ng/ml, respectively) were not significantly different (Caldwell et al., 1984).

Neotoma fuscipes has a sphenofrontal foramen for passage of the stapelial artery into the orbit (Hill, 1935); however, Carleton (1980) stated that this foramen was lacking. The subsquamosal foramen abuts the mastoid at the posterior edge as in *Castor*, but other rodents have the foramen surrounded by the squamosal (Hill, 1935). Unlike other rodents, no blood vessels pass through this

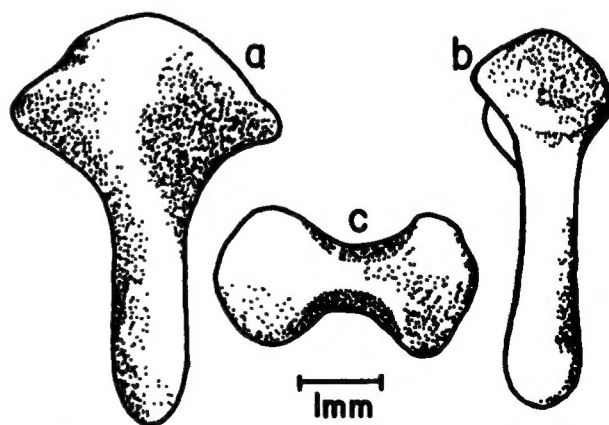


FIG. 3. Lateral (a), dorsal (b), and distal (c) views of baculum of *Neotoma fuscipes annectens* (redrawn after Burt and Barkalow, 1942).

foramen in *N. fuscipes*. There is a large stapelial foramen and the squamosal has a groove that merges with the sphenoidal fissure (Carleton, 1980).

Neotoma fuscipes has enlarged sebaceous glands at the oral angle and small apocrine sudoriferous glands (Quay, 1965). *N. fuscipes* also has an anal gland that produces a strong musk (Vestal, 1938).

Urine of *N. fuscipes* contained only crystals of struvite; no oxalate was detected (Emerson and Howard, 1978). The chlorine-ion concentration in urine of *N. fuscipes* tested during summer or acclimated to summer conditions (431.7 and 459.4 mEqCl⁻¹) was much greater than for those *N. fuscipes* tested during winter or acclimated to winter conditions (245.7 and 337.5 mEqCl⁻¹—Stallone, 1979). The urine-concentrating abilities of *N. fuscipes* are correlated with the variable amounts of water present in plants throughout the year (Stallone, 1979). The decrease in body mass and increase in urine-concentrating abilities of *N. fuscipes* in summer is an adaptation to less available water and higher temperatures in chaparral and coastal sage (*Artemisia*)-scrub communities it inhabits (Stallone, 1979).

Feces are elongated ellipsoids (Vestal, 1938). Mean width and length of fecal droppings were 3.6 mm and 9.1 mm for adult females and 4.8 mm and 11.9 mm for adult males (Vestal, 1938). Fecal-water content (\pm SE) for summer-acclimated *N. fuscipes* was $43.8 \pm 3.0\%$ (Stallone, 1979).

Means and ranges (in parentheses) for lengths (in cm) for some digestive-tract elements were: small intestine, 50 (48 – 52); cecum, 10 (8.5 – 11.1); and large intestine, 82 (70 – 94 —Kofoid et al., 1935). There are three to four Peyer's patches in the small intestine, a well-developed ileocecal valve, and a valve in the colon 44 mm posterior to the cecum. Means (\pm SE) and ranges (in parentheses) of the thicknesses of the well-defined cortical and inner and outer medullary zones of the kidney are 2.04 ± 0.06 mm (1.90 – 2.26), 1.88 ± 0.03 mm (1.75 – 1.97), and 5.65 ± 0.08 mm (5.30 – 6.01), respectively (Stallone, 1979). The renal papillae extend a short distance into the pelvis of the ureter (Stallone, 1979). The spleen is 7 by 25 mm. The liver is divisible into a large right lobe and a left lobelet; the middle of the left lobelet lies on top of the right lobe (Howell, 1926). *N. albigula* and *N. cinerea* have the opposite arrangement. The cubic capacity of the liver is 5 ml; for *N. albigula* and *N. cinerea* it is much greater. The thyroid gland is divided, one section on either side of the trachea; the sections are small and inconspicuous (Howell, 1926). The liquid secreted by the parotoid glands contains no mucin but is particularly rich in ptyalin (Howell, 1926). *N. fuscipes* has distinct cardiac and pyloric portions of the stomach (Kofoid et al., 1935). The stomach of *N. fuscipes* has a deep incisura angularis and is lined mainly with cornified squamous epithelium with a small area (diameter = 20 mm, thickness = 2 mm—Howell, 1926) of glandular epithelium opposite the base of the esophagus (Carleton, 1973; Howell, 1926).

Greatest zygomatic breadth is anterior in *N. fuscipes*, posterior in *N. albigula* and *N. cinerea*. The temporal ridges and fossae are smaller, pterygoid fossae narrower, angular processes shorter, and transverse mandibular fossae smaller than for *N. albigula* and *N. cinerea* (Howell, 1926). In comparison with these species, the inferior lamella of the sixth cervical vertebra is shorter, lumbar vertebrae longer, hypapophyses of the lumbar vertebrae higher, sacral vertebrae shorter, diapophyses of the caudal vertebrae larger, and diapophyses of the fifth caudal vertebra double (not single). *N. fuscipes* usually has a greater number of caudal vertebrae ($\bar{X} = 30.4$) than *N. albigula* or *N. cinerea*. The sternum is shorter, but has a longer manubrium in *N. fuscipes*. The tricipital fossa of the ulna is less well defined; the radius, innominate, and tibia longer; and fibula (to notch) shorter than in *N. albigula* and *N. cinerea* (Howell, 1926).

The sternofascialis muscle, absent in *N. albigula* and *N. cinerea*, occurs as a slender slip in *N. fuscipes*, but the temporalis, stylohyoideus, sternomastoideus, and omohyoideus are not as well developed. The medial and ventral scalenus muscles originate more anteriorly in *N. fuscipes* than in *N. albigula* and *N. cinerea*. The external oblique abdominal muscles are small in *N. fuscipes*. The spinotrapezius muscles, superior posterior-serratus muscles, and lateral rectus capitis muscles are larger than in *N. albigula* and *N. cinerea*. *N. fuscipes* has smaller teres minor muscles and gracilis muscles. The psoas minor muscles and gluteus muscles have narrower origins compared with those of *N. albigula* and *N. cinerea* (Howell, 1926). *N. fuscipes* has a hyoid apparatus characterized by the

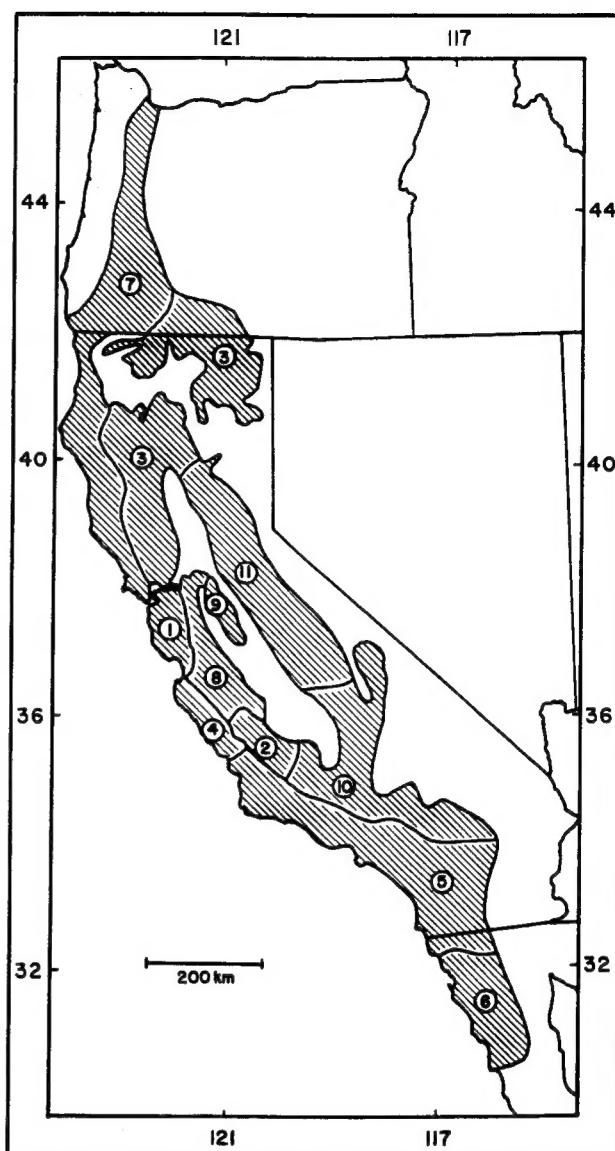


FIG. 4. Distribution of *Neotoma fuscipes*: 1, *N. f. annectens*; 2, *N. f. bullator*; 3, *N. f. fuscipes*; 4, *N. f. luciana*; 5, *N. f. macrotis*; 6, *N. f. martirensis*; 7, *N. f. monochrourea*; 8, *N. f. perplexa*; 9, *N. f. riparia*; 10, *N. f. simplex*; 11, *N. f. streator*.

presence of a tympanohyal in young animals, partially separated stylohyoideus and jugulohyoideus muscles, a medial pharyngeal constrictor muscle that originates only from the posteriorly projecting thyrohyals, and a styloglossus muscles that originates from the auditory meatus and stylohyal (Sprague, 1942). Rinker (1954) used *N. fuscipes* and *N. floridana* as a basis for the description of the myology of *Neotoma*, but did not make interspecific comparisons.

ONTOGENY AND REPRODUCTION. Testes begin to enlarge at about 6 months of age, but these males do not mate at that time. In California, the testes of captive males began to enlarge about 21 December (Wood, 1935); however, most enlargement occurred from 20 January to 7 March (Vestal, 1938). The testes are scrotal during the breeding season. In nulliparous females, the vaginal orifice is covered with a membrane that disappears in adults (Wood, 1935). There is no vaginal plug after mating (Donat, 1933; Wood, 1935).

Gestation lasts 33 days (Wood, 1935); Donat (1933) reported that gestation lasted only 28 days, however, she was uncertain of the exact day of copulation. Females produce one annual litter (Vestal, 1938); litter size averages 2.6 (range, 1–4). Bailey (1936) reported 2–4 embryos/female *N. fuscipes* in Oregon. The breeding season, based on presence of gravid females and recently born young,

extends from February through September (Bailey, 1936; Gander, 1929; Vestal, 1938).

In the laboratory, first copulations were observed on 26 January and the last on 12 April for both *N. f. macrotis* and *N. f. annectens* (Donat, 1933; Wood, 1935). Of 31 *N. f. macrotis* paired in 62 different combinations, 17 pairs copulated, but produced only two litters. Poor breeding success could have resulted from placing one animal into the cage of an established animal instead of placing both in a neutral enclosure (Wood, 1935). For five pregnant *N. f. macrotis* captured in southern California parturition was on 1, 7, 16, and 20 February and 4 March (Wood, 1935). The earliest date of parturition for *N. f. annectens* was 6 April (Donat, 1933).

Neonates are hairless, except for vibrissae, and colored dull red (Donat, 1933; Wood, 1935); G. N. Cameron (in litt.) indicated that neonates from southern California are gray. At birth, males weigh 12.5–13.3 g and females 12.8–13.8 g. Even before their eyes open, young have enough coordination to walk. Response to tactile stimuli by way of the vibrissae, digits, and feet is acute in young woodrats and increases with age (Vestal, 1938). Incisors of neonates are splayed allowing young to hold the conical-shaped nipple viselike between the teeth (Bleich and Schwartz, 1974; Vestal, 1938); by weaning, the incisors straighten (Vestal, 1938). Eyes of young open at 11–17 days of age and shortly thereafter, soft dorsal (gray) and ventral (white) fur appears (English, 1923; Vestal, 1938). Weaning begins at about 21 days when the young begin to eat the same foods as the mother (English, 1923).

ECOLOGY. *Neotoma fuscipes* consumed 43.7 ml of water/day in the laboratory when maintained at 20–23°C and 50–80% relative humidity. Water consumption ad lib. was 24.5 ml/100 g body mass (Lee, 1963); Carpenter (1966) reported that the minimum daily requirement for water was 10.2% of body mass at 50–80% humidity. When deprived of water, *N. fuscipes* cannot maintain body mass and will die within 4–16 days; average mass loss from onset of total water deprivation to death was 40%. Mean (\pm SD) body temperature for *N. fuscipes*, maintained at 22°C was $36.6 \pm 0.70^\circ\text{C}$. The thermal-neutral zone for maintenance of *N. fuscipes* is 20–25°C, with an upper critical limit of 35°C; at temperatures $>35^\circ\text{C}$, oxygen consumption increases approximately $0.1 \text{ cm}^3 \text{ g}^{-1} \text{ h}^{-1}$ for each 1°C increase in ambient temperature. The mean minimal consumption of oxygen is $0.79 \text{ cm}^3 \text{ g}^{-1} \text{ h}^{-1}$ (Lee, 1963).

Houses composed of sticks, bark, plant cuttings, and miscellaneous objects piled in a conical heap (English, 1923; Gander, 1929; Horton and Wright, 1944) are built below rocky bluffs (Emerson and Howard, 1978; Gander, 1929), in trees (1.2–7.6 m above the ground—English, 1923), on the ground (English, 1923), on north-facing hillsides (Parks, 1922), or on canyon slopes (Chew et al., 1959; Horton and Wright, 1944; Merritt, 1974) where brush, rock piles, or vegetative overstory are abundant (Fitch, 1947; Gander, 1929). Commonly, they are built in dense thickets of *Rubus*, *Rosa*, *Rhus diversiloba*, and *Urtica* (English, 1923). One stick house was built between the ceiling beams of an attic in Oregon (Roest, 1951). The major characteristics of house localities are dark surroundings, cool temperatures, low to medium humidity, and good cover (Linsdale, 1957). Houses are used for (Vestal, 1938) nurseries, protection, resting, self care, food storage, and social communications; also, Vestal (1938) considered them an adaptation to terrestrial life. *N. fuscipes* conserves energy by having large houses located for maximum protection from temperature extremes, nearby food supplies that lessen foraging time, and hoarding behavior that allows not only for detoxification of some plant species, but for relatively continuous high-volume feeding (Atsatt and Ingram, 1983).

Items reportedly used as supporting structures for houses are trees such as *Pseudotsuga menziesii*, *Malus fusca*, *Quercus garryana*, *Salix lasiandra*, *Acer macrophyllum* (English, 1923), *Q. dumosa* (Gander, 1929), *Juniperus occidentalis* (Murray and Barnes, 1969), and *Q. agrifolia* (Lee, 1963; Parks, 1922; Vestal, 1937); shrubs such as *Crataegus douglasii* (English, 1923), *Rhus laurina* (Gander, 1929), and *R. integrifolia* (M'Closkey, 1972); forbs such as *Eriogonum fasciculatum* (Gander, 1929); and railroad fences (English, 1923), an overturned washbasin, and a large bird nest (Gander, 1929). The pile of materials that compose the house may be so dense around a *Q. dumosa* that the trunk is completely obscured and only the branches protrude. Openings commonly are found where limbs of trees protrude and occur throughout the height of the house thus allowing air and sunlight to penetrate inside. The floors of these openings are scattered with petioles and other food waste-products.

The house is a maze of passageways from external openings to large central chambers. Sleeping nests usually are in an outer part of the house and have no external opening; houses may contain three or four nests (Gander, 1929). There always is a central food chamber and some houses have a separate latrine. Vestal (1937) found a chamber at the top of a house filled with fresh cuttings of *Sambucus*, *Sanicula*, and seeds of *R. diversiloba*. Numerous openings also are present at ground level. Commonly, paths go from ground-level openings of one house to those of several other houses (Gander, 1929). If a house is built on a hillside, passageways commonly penetrate the soil; many species of fungi grow in these passageways (Gander, 1929; Parks, 1922).

Stick houses averaged 118.1 cm (range, 35–203) tall in California (Gander, 1929; Vestal, 1938); houses taller than 101.6 cm seemed to require more maintenance (Linsdale and Tevis, 1956). The average basal diameter was 152.7 cm (range, 45–230—Vestal, 1938); Linsdale and Tevis (1956) reported an average of 243.84 cm. The average basal area of a stick house was 1.98 m^2 (Vogl, 1967). Each house represents the efforts of many generations of woodrats (Horton and Wright, 1944; Linsdale and Tevis, 1956) and may be occupied continuously for >13 years (Linsdale and Tevis, 1956). The 572 houses examined by Vestal (1938) had an average volume of 0.71 m^3 .

In some areas of California, stick houses occur in densities of 7.4–37.1/ha ($\bar{X} = 24.7/\text{ha}$ —Cranford, 1977; Vogl, 1967); however, Vestal (1938) reported densities as high as 57 houses/ha. Cranford (1977) reported that each dusky-footed woodrat averaged 1.8 houses/home range; the average (\pm SE) period of occupancy was 5 ± 3.5 months (M'Closkey, 1972).

Air temperatures measured inside and outside of stick houses, at 1300–1510 h, ranged from 22 to 28°C ; the mean (\pm SD) difference between ambient and nest temperatures was $0.7 \pm 1.0^\circ\text{C}$. Vapor pressure (\pm SD), measured at 1300–1510 h, was $0.466 \pm 0.059 \text{ mm Hg}$ inside and $0.377 \pm 0.041 \text{ mm Hg}$ outside of nests within stick houses. These values indicate that large stick houses of *N. fuscipes* are effective barriers to ventilation (Lee, 1963), despite numerous openings (Gander, 1929).

Neotoma fuscipes is a "habitat specialist in scrub and woodland communities" (Meserve, 1974:442) that occupies "relatively dense chaparral and broad-sclerophyll woodland, streamside thickets, and mixed coniferous forest with well-developed undergrowth" (Murray and Barnes, 1969:45). However, it may be captured as far as 14 m from the edge of chaparral (Bradford, 1976). In Oregon, *N. fuscipes* occurs in habitats that include a mixture of: *Abies grandis*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Juniperus*, *Purshia tridentata*, *Cercocarpus ledifolius*, *Alnus rubra*, *Q. garryana*, *Salix*, and *A. macrophyllum* interspersed with a heavy growth of shrubby undergrowth (Hammer and Maser, 1973; Nettleton, 1957; Walters and Roth, 1950).

In California, *N. fuscipes* occurs in chaparral (Cameron, 1971; Chew et al., 1959; Horton and Wright, 1944; Lee, 1963), coastal sage-scrub (Horton and Wright, 1944; M'Closkey, 1972; Murray, 1957; Spevak, 1983), clear-cuttings (Tevis, 1956), and dense woods (Murray and Barnes, 1969; Tevis, 1956). The coastal sage-scrub plant association is considered marginal habitat for *N. fuscipes* (M'Closkey, 1972). These plant associations include a mixture of some of the following: *Dryopteris arguta* (Merritt, 1974), *Pinus coulteri*, *Yucca whipplei*, *Ceanothus leucodermis*, *C. tomentosus* (Vogl, 1967), *Pinus sabiniana*, *Quercus douglasii*, *Rhus trilobata*, *Ceanothus cuneatus* (Murray, 1957), *Pseudotsuga menziesii*, *Populus trichocarpa*, *Prunus ilicifolia* (Horton and Wright, 1944), *Libocedrus decurrens*, *Cercocarpus ledifolius*, *Purshia tridentata*, *Artemisia tridentata* (Murray and Barnes, 1969), *Chlorogalum pomeridianum*, *Fritillaria lanceolata*, *Trillium ovatum*, *Rubus parviflorus*, *Psoralea physodes*, *Rhamnus californica*, *Heracleum lanatum*, *Trientalis latifolia*, *Diplacus aurantiacus* (Vestal, 1938), *Salix lasiolepis* (Horton and Wright, 1944; Vestal, 1938), *Juglans californica*, *Heteromeles arbutifolia*, *Ceanothus megacarpus*, *Hedera helix*, *Foeniculum vulgare*, *Vinca minor*, *Marrubium vulgare*, *Nicotiana glauca*, *Lonicera subspicata*, *Senecio mikanioides* (Spevak, 1983), *Corylus rostrata* (Cranford, 1977; Vestal, 1938), *Alnus rubra* (Cranford, 1977, 1982; Horton and Wright, 1944), *Lithocarpus densiflora* (Cranford, 1977), *Quercus agrifolia* (Atsatt and Ingram, 1983; Horton and Wright, 1944; Murray, 1957; Parks, 1922), *Q. chrysolepis*, *Acer macrophyllum* (Horton and Wright, 1944; Merritt, 1974), *Quercus dumosa* (Horton and Wright, 1944; Murray, 1957; Vogl, 1967), *Q. turbinella* (Cameron, 1971), *Q.*

wislizenii, *Ceanothus crassifolius*, *Garrya fremontii* (Horton and Wright, 1944; Vogl, 1967), *Eriogonum fasciculatum* (Atsatt and Ingram, 1983; M'Closkey, 1972; Meserve, 1974; Murray, 1957; Spevak, 1983), *Rubus ursinus* (Cranford, 1977; Merritt, 1974; Spevak, 1983), *R. vitifolius* (Cranford, 1977, 1982; Vestal, 1938), *Platanus racemosa* (Horton and Wright, 1944; Spevak, 1983), *Cercocarpus betuloides* (Cameron, 1971; Horton and Wright, 1944; Vogl, 1967), *Adenostoma fasciculatum* (Horton and Wright, 1944; Murray, 1957; Spevak, 1983; Vogl, 1967), *Lotus scoparius* (M'Closkey, 1972; Meserve, 1974; Spevak, 1983), *Rhus diversiloba* (Cranford, 1977, 1982; Merritt, 1974; Murray, 1957; Parks, 1922; Vestal, 1938), *R. integrifolia*, *R. laurina* (Atsatt and Ingram, 1983; M'Closkey, 1972; Spevak, 1983), *Acer negundo* (Cranford, 1982), *Opuntia occidentalis* (Atsatt and Ingram, 1983), *Umbellularia californica* (Cranford, 1982; Horton and Wright, 1944; Merritt, 1974; Spevak, 1983; Vestal, 1938), *Arbutus menziesii* (Merritt, 1974; Vestal, 1938), *Arctostaphylos glandulosa* (Horton and Wright, 1944; Murray and Barnes, 1969; Parks, 1922; Spevak, 1983; Vogl, 1967), *Salvia apiana* (Atsatt and Ingram, 1983; M'Closkey, 1972; Meserve, 1974), *S. mellifera* (Atsatt and Ingram, 1983; Horton and Wright, 1944; Murray, 1957), *Lonicera involucrata* (Cranford, 1977, 1982), *Baccharis pilularis* (Cranford, 1977, 1982; Parks, 1922; Vestal, 1938), *Artemisia californica* (Atsatt and Ingram, 1983; M'Closkey, 1972; Meserve, 1974; Spevak, 1983), and *A. douglasiana* (Linsdale and Tevis, 1956). Small forbs and grasses form the ground-level vegetation (Cranford, 1982). *N. fuscipes* (Fig. 4) and *Rhus diversiloba* have approximately the same geographic distributions (Gillis, 1971).

Information concerning the diet of *N. fuscipes* is based on food materials cached in stick houses; most such materials are plants readily available in the habitat surrounding houses. English (1923) reported ≤ 16 species of plants (composed of ≤ 132 cuttings of fresh material) cached in food chambers of houses. Individual food caches average 4.5 (range, 3–6) species of plants (Vestal, 1938); usually two or three foods compose the diet of *N. fuscipes* with one being dominant, usually *Quercus* when available (Atsatt and Ingram, 1983). Atsatt and Ingram (1983:140) concluded that "dietary uniformity may increase microflora efficiency, permitting increased ingestion rates, which are apparently necessary to maintain adequate nitrogen balance." Most of the diet includes evergreen sclerophyll vegetation high in fiber, tannins, and related polyphenolics (Atsatt and Ingram, 1983). Woodrats from areas vegetated with coastal *Salvia* or *Quercus* woodland selected *Quercus* foliage instead of other species even though *Quercus* contained 40% phenolics and 16% condensed tannin; their feces contained only 33% of the phenolics and 10% of the condensed tannin ingested even though only 55.3% of the *Quercus* was digested. Foliage of some plants (*Rhamnus californica* and *Heteromeles arbutifolia*) is detoxified by storage until dry (Atsatt and Ingram, 1983); however, vegetation from *Quercus* must be eaten fresh (≤ 10 days of collection) or the nutritive value decreases sharply (Chew and Woodman, 1974). Woodrats that ingested large quantities of *Quercus* were able to retain more nitrogen, possibly because proteolytic enzymes are induced by tannin or fiber in *Quercus*. Plants reportedly stored within food chambers are *Polystichum munitum*, *Chlorogalum pomeridianum*, *Rubus parviflorus*, *Fragaria vesca*, *Ceanothus thyrsiflorus*, *Scrophularia californica*, *Vicia exigua*, *Diplacus aurantiacus*, *Lonicera hispidula*, *Sambucus caerulea*, *Marah fabaceus*, *Baccharis pilularis* (Vestal, 1938), *Pteridium aquilinum*, *Pseudotsuga menziesii*, *Camassia leichtlinii*, *Corylus cornuta*, *Quercus garryana*, *Rumex mexicanus*, *Ribes lacustre*, *Rubus macropetalus*, *R. spectabilis*, *Physocarpus capitatus*, *Oemleria cerasiformis*, *Prunus virginiana*, *Malus*, *Malus fusca*, *Crataegus douglasii*, *Lathyrus polyphyllus*, *Geranium egeganum*, *Acer circinatum*, *Cornus occidentalis*, *Fraxinus latifolia*, *Hydrophyllum* (English, 1923), *Juniperus californica*, *Quercus turbinella* (Cameron, 1971), *Bromus tectorum*, *Festuca megalura*, *Alnus rhombifolia*, *Quercus chrysolepis*, *Eriogonum gracile*, *Ribes amaram*, *Lupinus longifolius*, *Cercocarpus betuloides*, *Rhus trilobata*, *Rhamnus californica*, *Ceanothus crassifolius*, *C. leucodermis*, *C. oliganthus*, *Arctostaphylos glandulosa*, *A. glauca*, *Fraxinus dipetala*, *Turricula parryi*, *Cryptantha intermedia*, *Monardella hypoleuca*, *Lonicera subspicata*, *Stephanomeria virgata*, *Garrya veatchii* (Horton and Wright, 1944), *Yucca whipplei*, *Romneya coulteri*, *Solanum xanti*, *Galium angustifolium* (Pequegnat, 1951), *Smilacina stellata* (English, 1923; Hammer and Maser, 1973; Vestal, 1938), *Salix lasiandra* (English, 1923; Hammer and Maser, 1973), *S. lasiolepis* (Horton and Wright, 1944;

Vestal, 1938), *Populus trichocarpa* (English, 1923; Horton and Wright, 1944), *Corylus californica*, *Ribes sanguineum*, *Rosa gymnocarpa*, *Rhamnus purshiana*, *Sanicula crassicaulis*, *Symphoricarpos albus* (English, 1923; Vestal, 1938), *Quercus agrifolia* (Atsatt and Ingram, 1983; Gander, 1929; Horton and Wright, 1944; Meserve, 1974; Vestal, 1938), *Q. dumosa* (Horton and Wright, 1944; Meserve, 1974), *Q. wislizenii* (Chew and Woodman, 1974; Horton and Wright, 1944), *Eriogonum fasciculatum* (Gander, 1929; Horton and Wright, 1944; Meserve, 1974; Pequegnat, 1951), *Ranunculus* (Hammer and Maser, 1973), *Clematis* (Gander, 1929; Horton and Wright, 1944), *Prunus ilicifolia* (Gander, 1929; Horton and Wright, 1944), *Amelanchier alnifolia* (English, 1923; Hammer and Maser, 1973), *Adenostoma fasciculatum* (Chew and Woodman, 1974; Gander, 1929; Horton and Wright, 1944; Pequegnat, 1951), *Heteromeles arbutifolia* (Atsatt and Ingram, 1983; Gander, 1929; Horton and Wright, 1944; Vestal, 1938), *Rhus diversiloba* (English, 1923; Gander, 1929; Horton and Wright, 1944; Vestal, 1938), *R. integrifolia* (Gander, 1929; Meserve, 1974), *R. laurina* (Gander, 1929; Pequegnat, 1951), *R. ovata* (Horton and Wright, 1944; Pequegnat, 1951), *Acer macrophyllum* (English, 1923; Horton and Wright, 1944), *Ceanothus verrucosus* (Gander, 1929), *Umbellularia californica* (Atsatt and Ingram, 1983; Horton and Wright, 1944; Vestal, 1938), *Arbutus menziesii* (English, 1923; Parks, 1922; Vestal, 1938), *Lonicera interrupta*, *Sambucus racemosa*, *Eriodictyon crassifolium* (Gander, 1929), *Salvia apiana* (Horton and Wright, 1944; Meserve, 1974), and *S. mellifera* (Chew and Woodman, 1974; Horton and Wright, 1944). Fungi also are part of the diet of *N. fuscipes*; it hunts for *Melanogaster*, *Hymenogaster*, *Hydnangium*, and mature *Hysterangium* and digs holes 153–350 mm deep to reach the mature fungus *Gautieria* and 103–153 mm deep to reach the mature *Elaphomyces* (Parks, 1922). *N. fuscipes* may practice coprophagy to increase digestive efficiency on marginal foods and to reinoculate the gut with microflora (Atsatt and Ingram, 1983).

Neotoma fuscipes is most numerous where tree cover is complete ($\geq 90\%$)—Vogl, 1967) and undisturbed by fire (Lee, 1963; Tevis, 1956) and least abundant in relatively open areas (Fitch, 1947); population densities decrease significantly as aridity increases (Spevak, 1983). Apparently, the greatest detriment to woodrat density is the removal of *R. diversiloba* and underbrush from occupied habitat (Linsdale and Tevis, 1956; Vestal, 1938); however, browsing and trampling by ungulates, flood, and drought also can be detrimental (Linsdale and Tevis, 1956). Reported population densities for woodrats, in undisturbed habitat, ranged from 5.1/ha in open habitat to 37.1/ha where the canopy is $\geq 90\%$ closed (Fitch, 1947; Horton and Wright, 1944; Merritt, 1974; Vogl, 1967); however, Wallen (1982) reported a population density of 45.2 woodrats/ha. Cranford (1977) reported population densities of 20/ha in late summer and 14/ha in winter. In a burned-over canyon in central California, Chew et al. (1959) found 39.5 dead *N. fuscipes*/ha.

Home-range areas for adult females ($\bar{X} = 1,924 \text{ m}^2$) and adult males ($\bar{X} = 2,289 \text{ m}^2$) were significantly different; home-range areas for juveniles averaged 1,719 m^2 . Home-range areas among females overlapped 25%, among males 15%, and for individuals of opposite sex 28%; however, during the breeding season home-range areas of individuals of opposite sex overlapped 57%. Before juveniles disperse, they commonly establish temporary home ranges (often around an unused house) overlapping the home-range area of the maternal female by as much as 62% (Cranford, 1977).

Neotoma fuscipes is preyed upon by *Mustela frenata* (Vestal, 1937, 1938), *Canis latrans* (Fitch, 1948), *Felis sylvestris* (Pearson, 1959; Vestal, 1938), *F. rufus* (Nussbaum and Maser, 1975), *F. concolor* (Towell and Maser, 1985), *Strix occidentalis* (Grinnell and Storer, 1924), *Tyto alba* (Fitch, 1947; Gander, 1929; von Bloeker, 1937), *Bubo virginianus* (Fitch, 1947; Maser and Brodie, 1966), *Buteo jamaicensis* (Fitch, 1947; Fitch et al., 1946), and *Crotalus viridis* (Fitch and Twining, 1946).

Neotoma fuscipes and its stick houses appear to be an integral component of the communities of which the species is a part; stick houses provide an excellent source of cover and food for many vertebrate and invertebrate commensals. The number of woodrat houses and species richness for small mammals, reptiles, amphibians, crustaceans, arachnids, and insects are directly related. In California, when *N. fuscipes* and its houses were removed the density of *P. truei* declined slightly; however, the density of *P. californicus* declined by 50% in the following 2 years (Cranford, 1982). Subsequently, as *N. fuscipes* repopulated the area, population densities

of *P. truei* and *P. californicus* increased as places for nest sites and refuges within stick houses increased. Mammals commensal with *N. fuscipes* in its stick houses were *Sorex ornatus*, *Notiosorex crawfordi*, *Sylvilagus bachmani*, *Peromyscus californicus*, *P. eremicus*, *P. maniculatus*, *P. truei*, and *Reithrodontomys megalotis* (Gander, 1929; Cranford, 1982; Vestal, 1938). Commensal reptiles and amphibians were *Sceloporus occidentalis*, *Elgaria multicarinatus*, *E. coeruleus*, *E. scincicaudus*, *Thamnophis ordinoides*, *Coluber constrictor*, *Masticophis lateralis*, *Pituophis melanoleucus*, *Hyla versicolor*, *Ensatina eschscholtzi*, *Batrachoseps attenuatus*, and *Taricha torosa* (Gander, 1929; Wood, 1944). Salamanders and newts live in the damp basal mulch of houses (Vestal, 1938). Commensal crustaceans, spiders, and insects were 2 species of Isopoda, 22 of Acarina, 2 of Araneida, 4 of Collembola, 3 of Orthoptera, several each of Psocidae and Trogidae (Corrodentia), 10 of Hemiptera, several of Dermaptera, 76 of Coleoptera, 1 of Lepidoptera, 12 of Diptera, 14 of Siphonaptera, 11 of Hymenoptera, and some unidentified Diplopoda and Chilopoda (Ashley and Bohnsack, 1974; Baker, 1949; Clover et al., 1989; Davis, 1934; Easton and Goulding, 1974; Furman, 1959; Gander, 1929; Higgins and Woolley, 1969; Redington, 1970; Vestal, 1938; Walters and Roth, 1950). Walters and Roth (1950) reported that Acarina were the most common (250/nest) and Pseudoscorpionidae (Arachnida), Siphonaptera, Cryptophagidae, and Staphylinidae (Coleoptera) and Formicidae (Hymenoptera) the next most common; 1–10 individuals of the remaining groups of insects were found in *N. fuscipes* nests and houses. During a 12-month period, Ashley and Bohnsack (1974) recovered 109,558 arthropods (100 species of 17 orders, 85% acarines) from sleeping nests within 72 stick houses. They reported dramatic seasonal changes in abundances of Mesostigmata, Prostigmata, Astigmata, and Cryptostigmata mites. In the chaff beneath sleeping nests, larvae of dipterous and lepidopterous insects, tenebrionids, and adult and larval forms of staphylinid beetles were found. Beetles (*Cibdelis blaschki* and *Eleodes parvicollis*), a millipede (*Julus hesperus*), and a snail (*Polygyra*) occurred in the damp basal mulch of houses (Vestal, 1938).

Other mammalian associates of *N. fuscipes* in Oregon include *Scapanus townsendii*, *Sylvilagus bachmani*, *Lepus californicus*, *Spermophilus beecheyi*, *Peromyscus truei*, *N. cinerea*, *Microtus californicus*, and *Mephitis mephitis* (English, 1923; Gabrielson, 1931; Hammer and Maser, 1973). In California, mammalian associates of *N. fuscipes* include *Didelphis virginiana*, *Sorex trowbridgii*, *Neotrichus gibbsii*, *Scapanus latimanus*, *S. townsendii*, *Sylvilagus audubonii*, *Lepus californicus*, *Aplodontia rufa*, *Thomomys bottae*, *Tamias merriami*, *T. townsendii*, *Spermophilus beecheyi*, *Sciurus griseus*, *Tamiasciurus douglasii*, *Glaucomys sabrinus*, *Perognathus longimembris*, *Chaetodipus californicus fallax*, *Dipodomys agilis*, *D. gravipes*, *Peromyscus boylii*, *N. cinerea*, *N. lepida*, *Clethrionomys californicus*, *Phenacomys longicaudus*, *Microtus californicus*, *Mus musculus*, *Procyon lotor*, *Mephitis mephitis*, *Taxidea taxus*, *Urocyon cinereoargenteus*, and *Odocoileus hemionus* (Cameron, 1971; Chew et al., 1959; Cranford, 1982; English, 1923; Gabrielson, 1931; Gander, 1928, 1929; Goldman and Moore, 1946; Grinnell and Orr, 1934; Lee, 1963; Linsdale and Tevis, 1951; MacMillen, 1964; McCloskey, 1972; Merritt, 1974; Meserve, 1974; Murray, 1957; Murray and Barnes, 1969; Pearson, 1959; Pequegnat, 1951; Pfeiffer, 1953; Smith, 1965; Tevis, 1956; Vestal, 1937, 1938).

Elgaria multicarinatus found in houses of *N. fuscipes* in southern California were infested with *Triatoma protracta* nymphs infected with the protozoan *Trypanosoma cruzi* (Wood, 1944). Nest fleas (Clover et al., 1989) in northern California and *N. fuscipes* (Hammer and Maser, 1973) in southern Oregon tested positive for antibodies for *Yersinia pestis*. In northeastern California, populations of *N. fuscipes* were severely decimated possibly by outbreaks of plague in 1928, 1934–1935, 1962, and 1966–1967 (Murray and Barnes, 1969), thus contributing to the disjunct distribution in that region (Fig. 4). *N. fuscipes* and the woodrat flea *Orchopeas howardi* reportedly were infected with the protozoan *Trypanosoma neotomae*. In woodrats, the infection lasted ≤ 8 months (usually 2–6 months); the animals exhibited no overt symptoms of the disease. Of 61 *N. f. annectens* trapped in central California 19.6% were infected; however, of 78 *N. f. macrotis* trapped in southern California, only 1.3% were infected (Wood, 1936). *N. fuscipes* is naturally infected with the bacterium *Pasteurella tularensis* in central California (Burroughs et al., 1945). In captivity, by day 4 or 5 after capture, some

individuals develop a fatal disorder characterized by prolapse of the lower intestine ≤ 152 mm beyond the anus (Gander, 1929).

Endoparasites recorded from *N. fuscipes* (Henry, 1932; Kofoid et al., 1935; Linsdale and Tevis, 1951) are the protozoans *Eimeria neotomae* and *E. residua* (oocytes in jejunum, ileum, and cecum at pH 6.6–7.3), *Trichomonas muris* (in small intestine, cecum, and colon at pH 6.72–7.50; occurs in area 25–458 mm below stomach), *T. caviae* (in jejunum, ileum, cecum, and colon at pH 7.20–7.88), and *Chilomastix* (in the cecum and colon at pH 7.0–7.5). The nematode *Trichuris neotomae* in the cecum (Chandler, 1945), and the trematodes *Nematodirus tortuosus* and *Andrya neotomae* in the small intestine (Tucker, 1942; Voge, 1946) also were reported.

Ectoparasites recorded from *N. fuscipes* are Anoplura: *Neohaematopinus neotomae* (Ferris, 1942); Acarina: *Dermacentor occidentalis* (Cudmore, 1986; Kohls, 1937), *Ixodes pacificus* (Cudmore, 1986; Easton and Goulding, 1974), *I. spinipalpis* (Cudmore, 1986), *I. angustus* (Easton and Goulding, 1974), *I. ricinus* (Vestal, 1938), *Tyrophagus*, *Proctolaelaps*, *Aplodentopus*, *Euryparusitus*, *Dermacarus spermophilus*, *Xenoryctes* (Cudmore, 1986), *Brevisterna ambulans*, *B. utahensis* (Keegan, 1949, 1951), *Androlaelaps fahrenheitsi* (Cudmore, 1986; Whitaker and Maser, 1985), *Eulaelaps stabularis* (Cudmore, 1986), *Haemogamasus reidi* (Cudmore, 1986; Whitaker and Maser, 1985), *Hypoaspis lubrica* (Cudmore, 1986), *Otodectes* (Vestal, 1938), *Radfordia neotomae* (Cudmore, 1986; Jameson and Whitaker, 1975), *Cosmochthonius reticulatus* (Higgins and Woolley, 1969), *Hirstionyssus breviseta* (Herrin, 1970), *Bakerdania*, *Myocoptes neotomae*, *Chatia setosa*, *Comatacarus americana* (Cudmore, 1986), *Euschoengastia ambocalis* (Loomis and Bunnell, 1962; Wrenn and Loomis, 1973), *E. criceticola* (Loomis and Bunnell, 1962), *E. obscura* (Wrenn and Loomis, 1974), *E. peromysci*, *E. pomerantzi* (Cudmore, 1986), *E. radfordi* (Loomis and Bunnell, 1962), *E. simulans* (Cudmore, 1986; Wrenn and Loomis, 1974), *Neotrombicula harperi* (Loomis and Bunnell, 1962), *N. caviticola* (Cudmore, 1986; Easton, 1975); Siphonaptera: *Aetheca wagneri*, *Eumolpianus eumolpi* (Lewis et al., 1988), *Anomiopsyllus falsicalifornicus* (Cudmore, 1986; Hubbard, 1947; Lewis et al., 1988), *A. congruens* (Stewart, 1940), *A. nudatus*, *Hystrichopsylla dippei* (Hubbard, 1947), *Meringis cummingi* (Stewart, 1940), *M. hubbardi* (Lewis et al., 1988), *Athyphloceras multidentatus* (Clover et al., 1989; Cudmore, 1986; Easton, 1983; Lewis et al., 1988), *Nosopsyllus fasciatus* (Vestal, 1938), *Catallagia sculleni* (Clover et al., 1989; Lewis et al., 1988), *Myodopsylla gentilis* (Lewis et al., 1988), *Megarhoglossus procus* (Cudmore, 1986), *Orchopeas sexdentatus* (Clover et al., 1989; Cudmore, 1986; Easton, 1983; Hubbard, 1947; Lewis et al., 1988), *O. howardi* (Wood, 1936), *O. caedens* (Hubbard, 1947), *O. nepos*, *Sternistomera alpina* (Lewis et al., 1988), *Opisodasys nesiotus* (Hubbard, 1947), *O. keeni* (Clover et al., 1989; Lewis et al., 1988), *Oropsylla montana* (Clover et al., 1989; Hubbard, 1947), *Malariae telchinus*, *Odontopsyllus dentatus* (Hubbard, 1947); and Diptera: *Cuterebra latifrons* (Catts, 1967; Sabrosky, 1986) and *C. lepvora* (Austen, 1933). Gander (1929) reported that ca. 50% of *N. fuscipes* had warbles of *Cuterebra* in spring and early summer; in autumn many were hosts to small white dipteran larvae. Dong and Eddy (1975) recorded the first *Paraicia pascuorum* (Diptera: Muscidae) in California from *N. fuscipes* carcasses.

Economic impacts of *N. fuscipes* are varied: fecal droppings are good quality fertilizer (Streator, 1930); some individuals strip bark from trees (Nettleton, 1957), but the species is not considered detrimental to reforestation (Tevis, 1956); and the species was used to determine the effectiveness of injecting liquid preservatives into whole animals in the field (Loomis, 1960). *N. fuscipes* reportedly was taken in Sherman live traps (Cranford, 1982; Merritt, 1974), size 201 Tomahawk folding traps, no. 1 Havahart traps (Wallen, 1982), and single-catch live traps manufactured by Young's Animal Trap Co. (Evans and Holdenried, 1943), although other traps may be satisfactory. Of 30 *N. fuscipes* captured with single-catch live traps, 13% were involved in double captures (Evans and Holdenried, 1943). Movements were studied by use of a subminiature light and small battery attached to the animals (Fisher and Cross, 1979) and by radiotelemetry (Cranford, 1977).

BEHAVIOR. Woodrats always urinate away from the nest; urination lasts ca. 5–6 s, and flows as a succession of small drops (Vestal, 1938). "Several bushels" of fecal droppings were found at the bases of 1.8-m-high houses of *N. f. annectens* and *N. f. streatori*

(Streator, 1930:318). Periodically, piles of fecal droppings are pushed from houses to the outside (Vestal, 1938). Vestal (1938) reported that for 516 houses combined, *N. f. annectens* produced 76.2 m³ of fecal droppings/year. He concluded that fecal droppings contributed significantly to the habitat. A captive adult female produced 1,008 fecal droppings (0.55 l) in 7 days at a rate of 144 fecal droppings/24 h (Vestal, 1938).

When disturbed within houses, *N. f. annectens* produced characteristic clattering sounds by rapidly vibrating the distal one-third of the tail on dried vegetation (Vestal, 1938) for ≥ 3 s at 10-s intervals. Sometimes shrill chattering sounds are made and animals tail-rattle on tree branches after escaping from their houses (Vestal, 1938). Woodrats use trails between houses as escape routes (Gander, 1929); when pursued they remain in the proximity of their houses (Parks, 1922). When captured, young *N. fuscipes* squeal but adults usually are silent (Gander, 1929). In the wild, combatants produce short, shrill squeals when attacking with the forefeet and make clicking and grating sounds with their teeth (Vestal, 1938). Nursing young (<20 days old) cling tightly to nipples and are dragged through trees, shrubs, and *R. diversiloba* when maternal females flee their houses (Gander, 1929; Parks, 1922; Vestal, 1938). Under duress females may dislodge young as they flee (Gander, 1929); young are usually retrieved within 2–4 h (Vestal, 1938). Adult males immediately vacate houses in which females with young seek refuge (Vestal, 1938).

In captivity, *N. f. annectens* commonly remained aggressive and difficult to handle (Donat, 1933; Wood, 1935), although an instance of cooperative behavior in the wild is recorded (Parks, 1922). *N. f. annectens* fight in the wild, especially during the breeding seasons, as demonstrated by torn pinnae and scars on the bodies of captured animals (Donat, 1933). *N. f. macrotis*, regardless of sex, exhibited violent antagonistic displays immediately upon detecting one another when paired in neutral arenas (Cameron, 1971). However, within populations of *N. f. macrotis* (Wood, 1935) and *N. f. monochoura* (English, 1923; Wallen, 1982) some animals are inquisitive and friendly, whereas others are furtive, distrustful, and aggressive. Most *N. f. macrotis* become calm and tractable in captivity; however, when an animal of the aggressive group is placed in the cage of another of the same group or the friendly group in an attempt to induce copulation, they fight causing severe or fatal damage (Wood, 1935). Postpuberal-castrated male *N. f. macrotis* exhibit as high a level of aggression in laboratory pairings as their intact counterparts (Caldwell et al., 1984). By placing animals in a multilevel enclosure of 8.4 m² in the laboratory, Kinsey (1971) was able to alter the territorial social behavior of *N. fuscipes* to a hierarchical organization, in which sex and size determined social rank. Frequency of aggressive attacks declined as the dominance hierarchy was established. When other individuals were introduced into these stable social hierarchies, they usually became the most subordinate animals, feeding during the day and hiding at night while resident animals were active. In small mammal communities in which it occurs, *N. fuscipes* is the behaviorally dominant rodent (MacMillen, 1964; Meserve, 1974).

The usual sitting posture for *N. fuscipes* is resting on the hindfeet with the forefeet against the chest; the tail is either arched over the body or pointed directly away from the body (Vestal, 1938). When walking, the tail is carried ca. 25 mm above the ground pointed directly away from the body and the ears are laid back (Vestal, 1938). A large male was observed to sit crosswise on an 8-mm-diameter branch and to use its tail to balance (Gander, 1929).

Neotoma fuscipes exhibits diel activity (English, 1923; Parks, 1922), although it is more active at night (Lee, 1963). Habitat use by *N. f. fuscipes* was related to density of cover; greatest activity was observed where vegetative cover was 75–100% (Cranford, 1977). *N. f. macrotis* exhibits the greatest arboreal tendencies of the 11 subspecies of *N. fuscipes* (Cranford, 1977; Howell, 1926).

There is no evidence that *N. fuscipes* exhibits homing. Of individuals released an average of 1,127 m from their capture sites >50% moved away from their initial capture site; females traveled an average of 837 m and males 949 m before recapture (Smith, 1965).

Houses are constructed where obstacles impede forward movement of a woodrat carrying sticks; when a large pile forms, passageways are cut into it (Linsdale and Tevis, 1956). Most house-building activity occurs during autumn and winter when availability of materials for construction is greatest (Linsdale and Tevis, 1956;

Parks, 1922). Usually, houses are occupied by a single adult or a female with young; however, Parks (1922) found evidence of two families sharing one house. *N. fuscipes* carries many unusual items into its houses: automobile bolts, bailing wire, bits of glass, bones, bread, brightly colored cloth or metal, broken bottles, crackers, dried prunes, dried dung, feathers, lace curtains, meat, mouse traps, nails, potatoes, salt chunks, old shotgun shells, shovel-handles, soap, socks, surveyor's stakes, tin cans, wall paper, and even a jelly roll (Bailey, 1936; Davis, 1934; English, 1923; Gander, 1929; Parks, 1922).

There is no evidence of polygamy in *N. fuscipes* (English, 1923). In the laboratory, tail-rattling by males, as they approached females, initiated copulatory behavior (Dial, 1987). Subsequently, females approached males, turned away, and assumed a position of lordosis (Dial, 1987; Wood, 1935); chases during mating were rare. First intromission occurred within 25–1,580 s (\bar{X} = 296 s) with ≤ 71 intromissions per copulatory sequence; females always terminated copulatory behavior by walking away from males. Intromissions lasted 0.5–4.5 s (\bar{X} = 2.4 s); there is no locking mechanism (Dial, 1987). Following copulation, both females and males groomed their urogenital areas (Dial, 1987). Wild-caught pregnant females destroyed or neglected litters born in captivity; however, females bred in captivity cared for their litters (Wood, 1935).

GENETICS. In *N. fuscipes*, $2n = 56$ and $FN = 82$, radically different from that of all other species of the subgenus *Neotoma*; the differences cannot be explained by Robertsonian processes (Baker and Mascarello, 1969; Mascarello and Hsu, 1976). There are ≥ 15 pairs of banded chromosomes (Baker and Mascarello, 1969). There is a large subtelocentric autosome and a small submetacentric autosome (Mascarello and Hsu, 1976). The X and Y chromosomes contain more heterochromatin than the other chromosomes and the heterochromatic arms of the X chromosome are considerably shorter than in other woodrats (Mascarello and Hsu, 1976). The missing proximal one-third of the acrocentric primitive G-band sequence of chromosome 2 and the change in centromere position in chromosome 3 are shared derived characters with *N. cinerea* and a pericentric inversion in chromosome 6 is a shared derived character with *N. lepida* (Koop et al., 1985). Baker and Mascarello (1969) and Mascarello and Hsu (1976) presented idiograms of *N. fuscipes* but provided no descriptions of them.

REMARKS. The generic name *Neotoma* is from the Greek prefix *neos* meaning new and *tomikos* meaning of or for cutting. The specific name *fuscipes* is from the Latin *fusc* meaning dusky and *pedalis* meaning of or belonging to the foot (Jaeger, 1978). The vernacular names of brush rats (Gander, 1929) or brushrats and traderrats (Parks, 1922) have been applied to *N. fuscipes*, the latter because of the folktale that *N. fuscipes* leaves something in place of items taken (Parks, 1922).

Neotoma fuscipes originally was placed in the subgenus *Homodontomys* (Goldman, 1910); however, based on the morphology of the baculum, Burt and Barkalow (1942) placed it in the subgenus *Neotoma*. Based on chromosomal comparisons, Koop et al. (1985) suggested that *N. fuscipes* be placed with *N. cinerea* in the subgenus *Teonoma*.

We thank G. N. Cameron and J. A. Cranford for comments on an earlier draft of this manuscript. This is Technical Paper No. 9150, Oregon Agricultural Experiment Station.

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